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SPECIAL ARTICLES

THE EXPLANATION OF A NEW SEX RATIO IN
DROSOPHILA

EXTRAORDINARY sex ratios have appeared at three different times in our stocks of *Drosophila*. Quackenbush described the first case.¹ Miss E. Rawls met with another case. Her results are now in press.² A third case has quite recently appeared in one of my other cultures not related to the last. During the past summer Miss Rawls turned over some of her stock to me. At that time some females were producing two females to one male, and other females equal numbers of both sexes.

If sex is determined by a factor in the sex chromosomes it seemed probable that some change had occurred in this chromosome. Several possibilities suggested themselves and were tested by means of the following crosses. I mated virgin females (red eyes) of Rawls's stock, in pairs, to white-eyed males. All the offspring had red eyes. Some of the F_1 females gave the 2:1 ratio. When these females were bred to white-eyed males again the following results were obtained:

Red ♀	Red ♂	White ♀	White ♂
448	2	452	374

The unusual ratio is evidently due to the almost complete disappearance of the red-eyed males, equality in all four classes being the normal expectation for this cross. On the face of these returns it seemed likely that some lethal factor must be contained in the single sex chromosome of the lost males. The lethal portion of this chromosome is derived from the red-eyed grandmother that gave the abnormal sex ratio. If this is the correct explanation, then, as the following analysis shows, all the red-eyed females in the last result should give a 2:1 ratio irrespective of the male to which they are bred. This, in fact, is the case. Similarly, the white-eyed females should give the usual 1:1 ratio; and this also proved true. The only doubtful point is the

case of the two red-eyed males. If the lethal factor contained in the chromosome in question should occasionally "cross over" from the red factor, then a red-producing chromosome would result, which, if it went into a male, should give a normal male. To test this these males were united to normal females and gave normal sex ratios. The daughters of these were then tested individually and all have produced normal ratios. The explanation holds. Conversely, there are expected a few white females due to crossing over that contain the lethal factor. The chance of obtaining one is approximately 1 in 200 times. As yet this test has not been carried out. The formulas which illustrate the relation just described are as follows:

Let X = the ordinary sex chromosome and x the sex chromosome that carries the lethal factor. The factor for red eye, R , and its allelomorph for white eyes, W , are carried by the sex chromosomes. The original female that gave a 2:1 ratio would have the formula $RX - Rx$ and the white-eyed male $WX -$. Then

Red ♀	$RX - Rx$
White ♂	$WX -$
<hr/>	
$RX WX$	= red ♀
$Rx WX$	= red ♀
$RX -$	= red ♂
$Rx -$	= —

Of the two kinds of red females we are concerned here only with $RxWX$. If she is mated to a white-eyed male the results are:

R_X	$- WX$	
WX	$-$	
<hr/>		
WX	WX	= white ♀
R_X	WX	= red ♀
WX	$-$	= white ♂
R_X	$-$	=

In both cases the male with the lethal factor does not develop, or dies. He does not, therefore, appear in the results except in those rare cases (the two cases above) where an interchange takes place between the sex chromosome in the female $Rx - WX$, so that there results $RX - Wx$.

¹ SCIENCE, 1910.

² Biol. Bulletin.

It is obvious on the other hand that half of the females also contain one sex chromosome that carries the lethal factor. They are saved by the other sex chromosome, but they will transmit the fatal dose to half of their sons who die and to half of their daughters who live.

The same test has been made with another sex-linked character, viz., miniature wings and the same results obtained. If, however, the lethal factor separates from the red-white factor ($R - W$) only once in 200 times it must be near that factor, on my hypothesis of the linear order of the factors in the chromosomes. If it does then we can calculate how often the crossing over for the wing factor should occur. In brief, we predicted the ratio of long and miniature-winged males that are expected in the back cross, *i. e.*, how many long-winged males would escape the fatal dose. The prediction was verified. For example, in F_2 there were obtained

$L \text{ } \text{f}$	$L \text{ } \text{m}$	$M \text{ } \text{m}$
910	156	243

The number of cross-over males is 156, the number expected for the total number (399) of males is 133; this excess of long males is in the direction which the known differences in viability of long versus miniature might produce.

Similarly for the sex-linked factor for "eosin eyes." This factor lies near to the factor for red (R), hence in an experiment similar to the one with white eyes, red-eyed males should be rare. Up to the present time, 411 F_2 eosin males have emerged and one red-eyed male. The expectation is two red males to 400 eosin males.

T. H. MORGAN

COMPLETE LINKAGE IN THE SECOND CHROMOSOME OF THE MALE OF DROSOPHILA

It has been shown recently¹ that the non-sex-linked factors that give black and wingless flies are linked to each other. In the F_2 generation (from P_1 black winged by gray wingless) there were produced:

¹ Morgan and Lynch, *Biol. Bull.*, Vol. XXIII., p. 174, August, 1912.

GW	BW	Gw
2,316	1,146	737

No black, wingless flies appeared which seemed due to close linkage between the factors in question. Yet, when F_2 gray, wingless females were tested by breeding to black, winged males quite a number of black flies were obtained in the first generation (15 to 125). The explanation offered was that "crossing-over" or breaking the linkage occurred so rarely that in the production of the F_2 generation no two wingless black gametes had happened to meet.

In order to test how often crossing-over occurred, the experiment was repeated, but this time the F_1 females and males were tested for cross-overs by mating them to black wingless flies. Thus, black, winged females were mated to gray, wingless males and gave F_1 gray, winged flies. The F_1 males were tested with black wingless females and gave:

$BW \text{ } \text{f}$	$BW \text{ } \text{m}$	$Gw \text{ } \text{f}$	$Gw \text{ } \text{m}$
514	478	355	366

These results show that there has been no crossing-over in the F_1 heterozygous males.

The converse cross was as follows: Gray, winged females were bred to black, wingless males and produced gray, winged males and females. The F_1 males were bred, as before, to black, wingless females, and gave:

$GW \text{ } \text{f}$	$GW \text{ } \text{m}$	$Bw \text{ } \text{f}$	$Bw \text{ } \text{m}$
213	171	154	123

Here again the combination that went into the F_1 male remained intact.

Similar crosses in which the F_1 females were tested gave a different result: When F_1 gray, winged females (out of black, winged females by gray, wingless males) were bred to black, wingless males there were obtained:

$BW \text{ } \text{f}$	$BW \text{ } \text{m}$	$GW \text{ } \text{f}$	$GW \text{ } \text{m}$	$Bw \text{ } \text{f}$	$Bw \text{ } \text{m}$	$Gw \text{ } \text{f}$	$Gw \text{ } \text{m}$
696	717	305	273	180	127	606	511

The converse cross, viz., F_1 , gray, winged females (out of gray, winged females by black, wingless males) were bred to black, wingless males and gave:

$BW \text{ } \text{f}$	$BW \text{ } \text{m}$	$GW \text{ } \text{f}$	$GW \text{ } \text{m}$	$Bw \text{ } \text{f}$	$Bw \text{ } \text{m}$	$Gw \text{ } \text{f}$	$Gw \text{ } \text{m}$
222	191	1,018	928	668	657	202	146

Adding the last two results together, it is